THE METHOD OF FEEDING OF CHAETOPTERUS

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Introduction

Ciliated currents present on the surface of animals, when examined under artificial conditions, are seldom, if ever, typical of the animal in its natural environment. Failure to recognize this fact and failure to observe the presence of mucus and note its importance in the feeding process have given rise to many erroneous descriptions of the feeding mechanism of various marine invertebrates. In conformity with the statement made in *Science* (MacGinitie, 1937), the feeding activities of many marine invertebrates have been investigated (including tunicates, pelecypods, gastropods, annelids and coelenterates), and descriptions of the feeding activities of these animals will follow as soon as they can be prepared for publication. This paper will deal with the feeding of the annelid *Chaetopterus variopedatus* Rénier et Claparède.

Because of its wide distribution and its usefulness as a source of embryological material, *Chaetopterus* is well known both abroad and in this country. Also, because of its unusual and somewhat bizarre structure, it has created a great deal of interest from both an anatomical and a natural history point of view (Laffuie, 1890; Enders, 1909). However, no paper that I have seen has given the correct method of feeding of this animal.

Feeding Method

The structures concerned with the feeding activities of *Chaetopterus* are the peristomial funnel with its lips, the mouth, the dorsal ciliated groove, which ends in the dorsal cupule of the thirteenth segment, the pair of aliform notopodia of the twelfth segment, and the three fans of the fourteenth, fifteenth and sixteenth segments (see Fig. 1).

In preparing to feed, *Chaetopterus* approaches one or the other end of the leathery U-shaped tube in which it lives and spreads its aliform notopodia out against the sides of the tube. It then begins to secrete mucus from the inner walls of these notopodia, the secretion beginning at the distal ends and proceeding inward toward the body. The cilia of the inner surface of the notopodia carry the mucus across the

opening in a sheet from the distal ends to the body of the worm, whence it is carried posteriorly as a bag by the ciliated groove to the dorsal cupule, where the closed end of the mucous bag is taken into the cup or concave surface of this organ. This creates an elongated bag of mucus, the anterior end of which is fastened to or continuous with the glands lining the inner surface of the aliform notopodia, and the closed posterior end of which is held by and rolled up within the dorsal cupule.

A current of water is now maintained through the burrow by the activity of the three fans just posterior to the dorsal cupule. Since

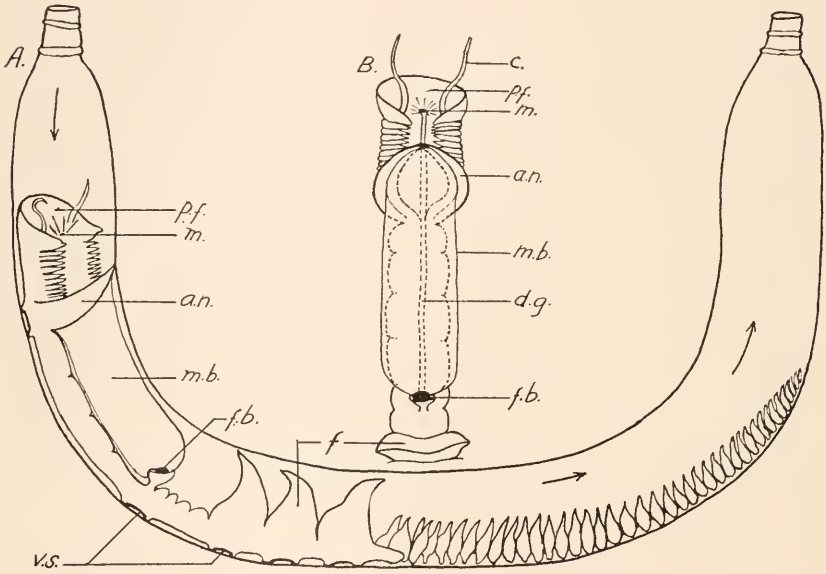

FIG. 1. *A*, *Chaetopterus variopedatus* within its tube, feeding; *B*, dorsal surface of anterior portion of worm. *a.n.*, aliform notopodium; *c.*, cirrus; *f.*, fans; *f.b.*, food ball being rolled up within the dorsal cupule; *d.g.*, dorsal ciliated groove; *m.*, mouth; *m.b.*, mucous bag; *p.f.*, peristomial funnel; *v.s.*, ventral suckers.

the walls of the burrow are completely in contact with the body of the animal and the aliform notopodia at the anterior end of the mucous bag, it is necessary for the current of water to pass into the bag, out through its sides, and thence along the body of the worm, and ultimately to issue from the burrow at the opposite end. While the current is being maintained by the fans, mucus is continuously secreted at the anterior end of the bag, and, at the same rate, the posterior end is rolled into a ball within the dorsal cupule by the cilia of its inner surface. Since all water entering the burrow while a mucous bag is

present passes through the walls of the bag, the mucus removes from the current all solid particles, whatever their size. It is these particles which lodge on the inner surface of the mucous bag that constitute the food of *Chaetopterus*. It consists mainly of detritus (organic debris and bacteria) stirred up from the surface of the ocean or estuarine bottom by wave action, currents, other animals, etc.

Because the entrances to the tube of *Chaetopterus* are considerably constricted, no very large particles find their way in with the feeding current. Such that do are usually detected by the peristomial cilia of the worm and are passed out at the sides of the worm anterior to the aliform notopodia, which are lifted to allow the material to pass, and so do not find lodgment in the mucous bag. Since the mucus of the bag is being secreted continuously, and at the same time the posterior end is being rolled into a ball in the dorsal cupule, it is evident that the entire bag is constantly being renewed, and that the posterior portion is much more heavily laden with food than is the anterior.

When the ball of mucus and food in the dorsal cupule reaches a certain size, the anterior end of the mucous bag is cut off from the notopodia, and the dorsal cupule continues to rotate the ball until the remainder of the bag is completely (or, occasionally, only partly) rolled up. The dorsal cupule is then turned anteriorly and stretched forward somewhat to expel the ball of food onto the posterior end of the dorsal groove. At the same time the action of the cilia of the groove is reversed, and the bolus of mucus with its entrapped food is carried forward along it to the mouth, where the bolus is enveloped by the lips and swallowed.

The size of the bolus of food depends upon the size of the dorsal cupule, and, therefore, upon the size of the animal. For a *Chaetopterus* about 6 inches long the food ball averages about 3 mm. in diameter. When *Chaetopterus* is feeding there is some variation in the length of its body, particularly in that portion between the head and the dorsal cupule, and, therefore, the length of the mucous bag will vary in the same animal at different times.

The following figures are given for a worm 142 mm. in length, measured during a time when the animal was feeding. Fifteen millimeters posterior to its point of origin, the width of the mucous bag was 6 mm., and the dorso-ventral diameter at the same point was 7 mm. The length of the mucous bag was 37 mm. The rate of secretion of this bag was approximately 1 mm. per second. While the worm was feeding the number of beats for any one of the three fans was 64 per minute, and this rate was the same for this particular

worm as observed on successive days over a period of several weeks. Although the rate of beating of the fans is quite uniform for any one worm, it varies with individuals, for another worm maintained a rate of 52 beats per minute. From the beginning of the spinning of the mucous bag to the ingestion of the bolus of food required, on the average, 17 minutes, and varied only plus or minus 1 minute from this average.

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